

Responses of Two Haliotid Gastropods (Mollusca),
Haliotis assimilis and *Haliotis rufescens*,
to the Forcipulate Asteroids (Echinodermata),
Pycnopodia helianthoides and *Pisaster ochraceus*

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(Plates 50, 51; 2 Text figures)

INTRODUCTION

SINCE 1949 THE STUDY OF RESPONSES of gastropods stimulated by asteroids has received much attention. The stimulating substance is liberated from the tube foot epidermis (BULLOCK, 1953; FANGE, 1963; FEDER, 1963, FEDER & LASKER, 1964; KOHN, 1961; MARGOLIN, 1964 a, b; YARNALL, 1964). Some evidence (FEDER, 1959, 1963; MARGOLIN, 1964 a, b) indicates that the response is part of a predator-prey escape pattern. Other animals tested exhibit similar responses but information is lacking as to their exact relationships with the asteroids. Responses to asteroids are not limited to gastropods. Experiments with pelecypods (RAY, 1959), actinozoans (ROBSON, 1961, 1963; YENTSCH & PIERCE, 1955) and other echinoderms (MACGINITIE & MACGINITIE, 1949) also showed responses.

Cox (1962) lists a zone from the intertidal to 540 feet as the depth range for *Haliotis rufescens*, with the majority of animals found at 20 to 50 feet. The range of *Haliotis assimilis* is given as 10 to 120 feet with major concentrations between 70 and 100 feet. These abalones overlap in their habitats, but *H. assimilis* is found in much smaller numbers. LIGHT (1954) lists *Pisaster ochraceus* and *Pycnopodia helianthoides* as intertidal animals but *Pisaster ochraceus* usually does not extend much beyond the intertidal, while *Pycnopodia helianthoides* is a permanent resident of subtidal waters. Dredging in Puget Sound, Washington, rarely produced a specimen of *Pisaster ochraceus* from the deeper waters, yet large numbers of *Pycnopodia helianthoides* were easily obtained from like

depths. The earlier work of BENNETT (1927) and later experiments by BULLOCK (1953) and FEDER (1963) indicate that haliotid gastropods respond to stimulation by asteroids.

For this study only the common forcipulate sea stars in the intertidal (*Pisaster ochraceus*) and the subtidal (*Pycnopodia helianthoides*) were used to initiate responses in the intertidal abalone (*Haliotis rufescens*) and a subtidal abalone (*H. assimilis*).

METHODS AND MATERIALS

Laboratory experiments were carried out at the Brebes Marine Laboratory, Morro Bay, California. Since 1964 this private facility has been concerned with the feasibility of commercially raising *Haliotis rufescens* and related species of abalone. Several hundred abalones of several sizes and species are available. Specimens of *H. rufescens*, for instance, range from 0.5 mm to 28 cm in shell length.

Holding tanks (24" x 48" x 18"), water tables (96" x 24" x 4"), and supplementary trays (36" x 24" x 3") are resined plywood. The supplementary trays nest into the holding tanks and water from the trays cascades into the tanks. Several of the supplementary trays were placed on supports and supplied with running sea water from the system. By changing the position of the inlet hose a stream of water could be directed anywhere across the tray, then drained into the main drain channel. To minimize current interactions the hose could be removed. This permitted star-liberated substances to diffuse normally throughout

the water or to be directed at the experimental abalone. Trays were scrubbed and filled with clean sea water after each experiment. Animals were rotated so that several days elapsed between successive stimulations for a particular animal. After testing, very sensitive animals like *Haliotis assimilis* were kept in separate tanks away from untested animals.

An abalone was placed on the tray in the water stream and allowed to become quiet. To test for diffusible substances, the asteroid was then placed in the water stream near the hose end. In a subsequent test the abalone was checked for its ability to react to diffused substances in quiet water. Each test was repeated. Experiments were also performed, in duplicate, in which the tube feet, ambulacral grooves and aboral epidermis of the stars were touched to the tentacles, epipodium and foot of the abalones. Other tests are described in the text.

Species of animals used:

Gastropoda (Prosobranchia)

Haliotis assimilis DALL, 1878

Haliotis rufescens SWAINSON, 1822

Asteroidea (Forcipulata)

Pisaster ochraceus (BRANDT, 1835)

Pycnopodia helianthoides (BRANDT, 1835)

Haliotis is a prosobranch gastropod, its limpet-like shell bearing a row of small holes to allow a more direct exit of the exhalant current from the mantle cavity. The animal is benthic in nature, moving slowly over rocks on the bottom on a broad, muscular foot as it feeds on algae.

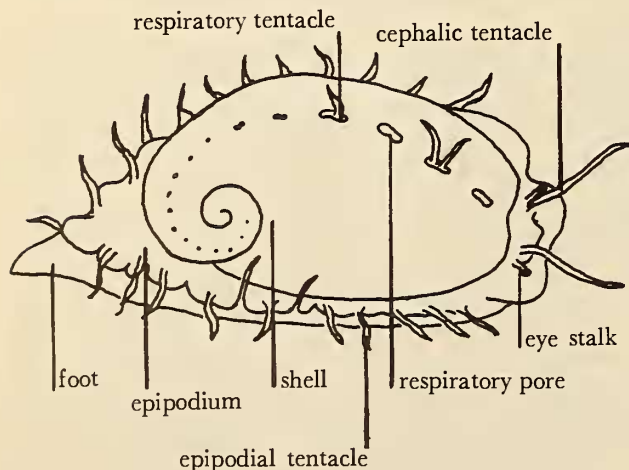


Figure 1

Haliotis spec.

A raised collar, the epipodium, encircles the foot dorsally and bears numerous tactile epipodial tentacles. The head has three pairs of tentacles: a short and a long pair of tactile cephalic tentacles and a more anterior pair with eyes at the tips. Several mantle tentacles project through the respiratory pores in the shell (see Text figure 1).

Forty-one individuals of *Haliotis assimilis* and 105 of *H. rufescens* were tested; 9 *Pisaster ochraceus* and 4 *Pycnopodia helianthoides* were used. Abalones tested consisted of mixed populations: freshly-caught animals, specimens collected and then raised in the laboratory, and animals raised from zygotes obtained from laboratory stock. No attempts were made in these experiments to determine differences between freshly-caught and laboratory-raised animals. All stars and abalones were obtained from the intertidal and subtidal waters off Morro Bay and Cayucos, California.

RESPONSES OF *Haliotis assimilis* to *Pycnopodia helianthoides*

Stream Responses

Specimens of *Haliotis assimilis* were placed on the tray in the stream of water, approximately 30 cm from the inlet hose. *Pycnopodia helianthoides* was held against the hose end and allowed to attach. The water stream passed over the oral surface of the star, down the table and over the abalone. Within 25 seconds (average time 15 seconds) the abalone extended the cephalic tentacles to maximum length (Plate 51, Figure 9), vibrating the tips rapidly and sweeping the tentacles back and forth through the water. The epipodium was protruded from beneath the shell within 36 seconds (average 25 seconds), its tentacles waving about in the water, the lobes swelling and extending stiffly from the body. Movement in an anterior direction began within 70 seconds (average 35 seconds), the animal moving randomly to the left, right, or straight ahead. Speed of locomotion increased with time, until the abalone was moving at several times normal speed. As the animal moved away from the stimulation on a left or right pathway the shell usually would be lifted away from the foot and be twisted rapidly back and forth through an arc from 30° to almost 180° (Plate 50, Figure 1). Depending on the sensitivity of the particular animal this twisting would start and stop several times as the animal moved away. The abalone moved rapidly to the edge of the tray, then along the side of the tray to a corner, or perhaps half-way or completely around the tray. Contact with the edge or corner of the tray usually produced a climbing reaction, with the animal moving up the side of the tray out of the water, and over the edge to fall on

the floor. Plate 50 shows a series illustrating these reactions. A majority of the animals tested also liberated quantities of a viscid mucus from the respiratory pores during flight (Plate 50, Figure 2). Animals re-encountering the star during flight recoiled sharply upon minimal contact, turned quickly away, and began a new flight response. In no case did an abalone crawl over the star to escape; it always recoiled and then moved away to left or right. The rapid locomotion noted barely resembled normal gliding movement. The anterior portion of the foot was raised from the substrate and extended far ahead, giving a leaping effect. The foot and body rocked from side to side as the animal moved. The margin of the foot undulated rapidly and the shell was usually held above the body in a mushrooming effect.

The above set of responses occurred with every specimen of *Haliotis assimilis* tested with *Pycnopodia helianthoides*; variations in speed of response occurred, but the pattern remained fairly constant. Experiments using the stream of water without a sea star elicited no response.

Responses to Contact

Contact was either effected manually by the observer, or randomly, the abalone being allowed to encounter the asteroid as it moved about. No significant difference was observed in comparing these contact responses. Contact with either tube feet or aboral epidermis of the asteroid always elicited positive responses. Contact was as minimal as possible, usually a slight touch.

Responses to contact followed the same pattern as with stream reactions, with all abalones tested. Plate 50, Figure 3 shows both twisting and climbing induced by contact with tube feet. Flight initiated by contact with tube feet was always away from the point of stimulation; anterior if the posterior epipodial tentacles were touched, left when touched on the right side, right when stimulated on the left, and posteriorly when cephalic tentacles were contacted. The abalone did not creep over the star in avoiding it, and in moving along the side of the tray above the star the shell was held away from the surface of the star.

A summation of contact responses is presented in Figure 2, Diagram a. The abscissa indicates the shell length in centimeters, the ordinate the strength of flight response. The strength of the response is indicated by an arbitrary scale ranging from 0 (no response) to 10 (full flight response: extremely rapid locomotion; shell twisting; emission of mucus; and climbing reaction). Regardless of size, specimens of *Haliotis assimilis* reacted with strong flight responses. All responses were 8 or above in strength, indicating that contact with a star was a major irritation effecting the responses.

Larger animals responded more slowly (50-70 seconds) to initial stimulation, but full flight responses (8-10) resulted. The upper size limit for *Haliotis assimilis* is 15 to 16 cm. Smaller animals (3-8 cm) continued to react for longer periods of time than larger ones, sometimes for as long as 30-40 minutes after being tested. Animals returned to holding tanks after testing stimulated flight responses in other abalones present. *Haliotis assimilis* touched briefly on the posterior tentacles by the tube feet of a small *Pycnopodia helianthoides* crawled rapidly along an eight-foot water table, against the water flow, climbing the far edge of the table and falling to the floor. During this travel it crawled over and touched two other abalones: one *H. rufescens* and one *H. assimilis*. Within 6-10 seconds the second *H. assimilis* also crawled to the near edge of the table, and over, and fell to the floor; *H. rufescens* displayed no response. A third *H. assimilis*, six feet away from the stimulation point and one foot to one side of the crawling abalone responded without contact within 15 seconds after the passage of the stimulated abalone. Several repetitions yielded like results.

The most rapid and also strongest flight responses resulted from stimulations of the posterior epipodial tentacles; lesser responses occurred on stimulation of the lateral or anterior epipodial tentacles. Stimulation of the posterior tentacles during flight usually caused the specimen to "surge" ahead, sometimes almost in a leaping manner. The cephalic tentacles showed sensitivity upon initial contact, but secondary stimulation during flight did not give as strong a response as secondary stimulation of epipodial tentacles. Flight was also accelerated by secondary stimulation of the posterior respiratory tentacles (extending through the posterior pore); stimulation of the anterior respiratory tentacle(s) gave a somewhat weaker response. Touching either the epipodial surface or the foot with the tube feet of the star resulted in a positive response.

Flight response continued up to 35-40 minutes from stimulation; flight length in centimeters exceeded 250 to 260 cm.

Repeated stimulation at five-minute intervals showed that *Haliotis assimilis* was still responding positively with little drop in strength of response after 195-230 minutes. FEDER (1963) and BULLOCK (1953) mention that after several stimulations the gastropod becomes desensitized and fails to respond. Mucus emitted by *H. assimilis* fouled the aboral surface of the asteroid to the point where it was felt that continuation of the experiment was useless. MARGOLIN (1964a), using *Diodora aspera* and *Pisaster ochraceus*, noted complete cessation of response after 320 to 390 minutes.

Pycnopodia helianthoides was allowed to remain in a dish of sea water for 30 + minutes. This "sea-star water" was then pipetted over *Haliotis assimilis*. Within 15-25 seconds a typical flight pattern was exhibited. Response strength in these experiments was 8 to 10 for all abalones tested.

Isolated tube feet induced the same response as contact with tube feet on the sea star. When pipetted into the water the detached tube feet produced a flight response immediately upon contact with an abalone. When none of the tube feet touched an abalone a response was observed after 60-70 seconds.

When glass, metal or wood probes were used to stimulate the specimens no flight response was noted; clamping down of the animal and tentacle retraction resulted. When, however, the probes were first rubbed over the oral surface of the sea star, subsequent contact produced a weak (6-7) response. Touching the foot, tentacles and epipodium with empty shells of *Tegula funebris*, *Acmaea* spp., *Haliotis* spp., and *Mytilus californianus* gave negative results.

RESPONSES OF *Haliotis assimilis* TO *Pisaster ochraceus*

Stream Responses

Time of responses to a stream of water crossing the oral surface of a star was much slower with *Pisaster ochraceus* than with *Pycnopodia helianthoides*. Of 41 abalones tested, 29 showed no significant tentacle activity for periods ranging from 1 to 6 minutes. When tentacle activity occurred, it was followed by minimal epipodial activity, extension from under the shell, and slow back-and-forth movement. After 1 to 6 minutes the abalone sometimes moved away from the star in a 90° to 180° turn, then became quiet. Of 41 animals tested, 16 displayed tentacle activity alone, 22 exhibited tentacle and turning reactions, and 13 gave typical flight responses of 3-5 strength, consisting of flight only; none of the other responses noted for *Haliotis assimilis* occurred. Flight responses were displayed only by animals smaller than 9 cm.

Responses to Contact

Figure 2, Diagram b shows contact responses of subject animals. Over 50% of the animals showed a response below 8 in strength. Specimens above 10 cm in length also showed a 50% response; 8 gave responses above 6, while 8 indicated a response below 6 in strength. This is in contrast to the reaction with *Pycnopodia helianthoides* where all animals exhibited strong flight responses. Only 1 of the smaller abalones (below 10 cm) gave a negative response; the rest were 5 or above in strength of responses. Flight responses when elicited showed the same pattern as with *Pycnopodia helianthoides*; the responses, however, took longer to initiate. Several stimulations were often required to give a flight response, and often the responses of shell twisting, mucus emission, and climbing occurred only after stimulation during flight. Differences in the sensitivity of the cephalic, epipodial and respiratory tentacles resulted as they did with *Pycnopodia helianthoides*; positive responses were also observed when the epipodium or foot of the abalone was touched by tube feet.

Specimens of *Haliotis assimilis* more than 10 cm in shell length exhibited an almost negative reaction to initial contact with tube feet or aboral epidermis; when the tube feet touched the foot or epipodium the abalone usually clamped down firmly (Plate 50, Figure 6). Continued stimulation sometimes produced a strong pushing reaction of the abalone shell against the arm of the star. In some instances this was repeated several times, after which the star moved away. Larger animals utilized this pushing action and the violent twisting of the shell already described instead of flight. Specimens below 10 cm in length usually fled with shell twisting accompanying the flight response. Usually only the tube feet of *Pisaster ochraceus* evoked a positive response. Stimulations with the aboral epidermis seldom produced flight responses, sometimes a shell twisting response, but usually only minimal tentacle activity. In several cases the abalone crawled over the aboral surface of the sea star; it did not crawl over the up-turned oral surface. When forced to crawl over the aboral surface of asteroid arms the abalone did so very rapidly, with the shell held high above the foot. "Sea-star

Explanation of Plate 50

RESPONSES TO *Pycnopodia helianthoides*

Figure 1: *Haliotis assimilis* twisting shell.

Figure 2: *Haliotis assimilis* liberating mucus.

Figure 3: *Haliotis assimilis* twisting and climbing.

Figure 4: *Haliotis rufescens* showing posterior epipodium covering response.

Figure 5: *Haliotis rufescens* showing posterior respiratory tentacle epipodial covering response.

Figure 6: *Haliotis rufescens* (10.3 cm) clamping down.

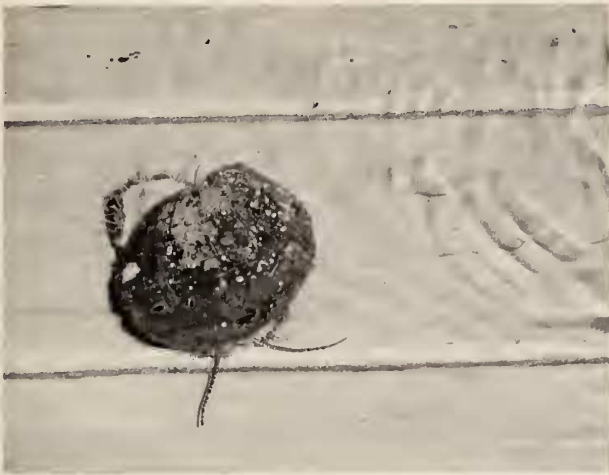


Figure 1

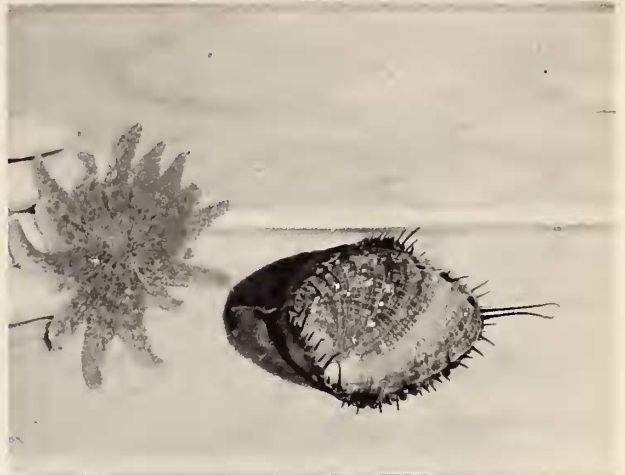


Figure 4



Figure 2



Figure 5



Figure 3

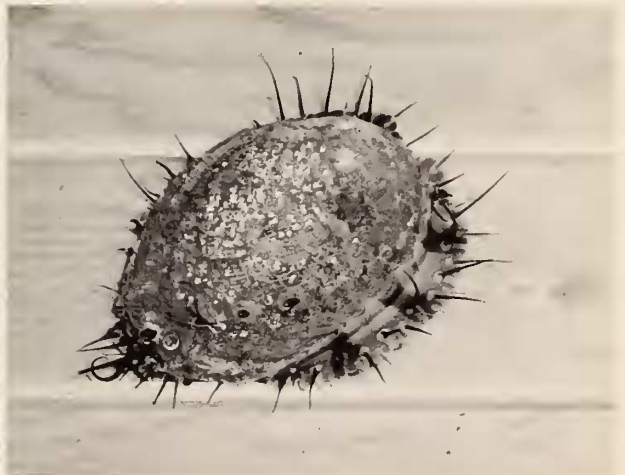


Figure 6



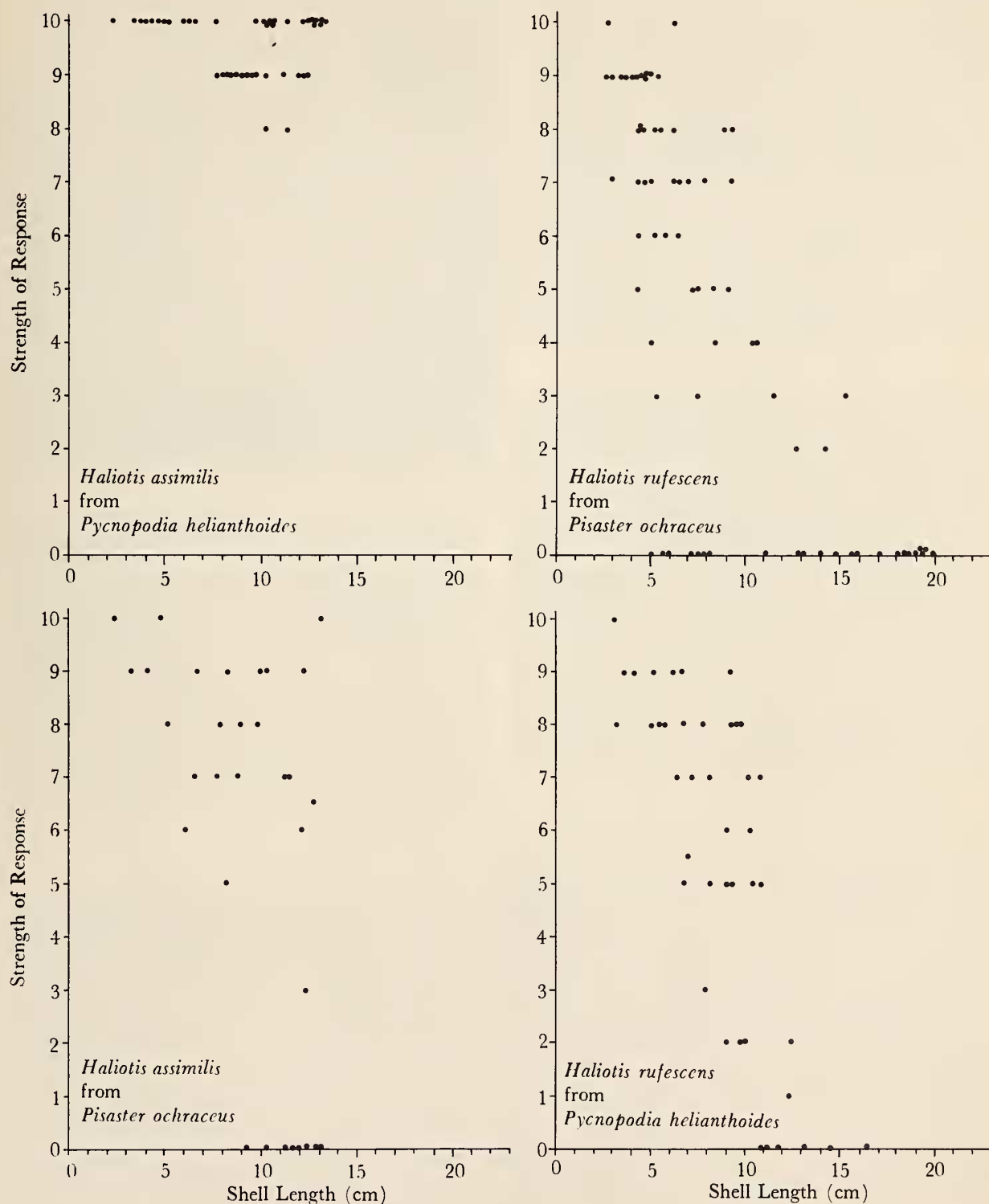


Figure 2

Flight Responses to Tube Feet Contact.

Diagram a: *Haliotis assimilis* from *Pycnopodia helianthoides*.Diagram b: *Haliotis assimilis* from *Pisaster ochraceus*.Diagram c: *Haliotis rufescens* from *Pisaster ochraceus*Diagram d: *Haliotis rufescens* from *Pycnopodia helianthoides*

Strength of response is based on an arbitrary scale measured in terms of: speed of flight responses, shell twisting, mucus emission, climbing out of experimental tray.

water" pipetted over 34 animals gave flight responses in 6 abalones; others showed only tentacle and epipodial activity, with some side-to-side turning. Stimulation with glass, metal and wood probes and with empty shells induced no significant responses. Stimulation with these objects, after they were rubbed over the oral surface of the sea star gave weak responses in a few instances.

RESPONSES OF *Haliotis rufescens* to *Pisaster ochraceus*

Stream Responses

Time lags before responses ranged from 48 seconds (in the smaller animals) to 5 minutes (in the larger [10 to 15 cm]) ones. Animals larger than 15 cm were not tested in the experimental tray as the water was not deep enough to cover their shells. Of 21 larger animals tested, 8 showed some tentacle activity, 7 turned away 90° to 180°, and 6 showed a minimal flight response, without shell twisting, mucus emission, or climbing reactions. The smaller animals (below 10 cm) showed flight responses. Animals larger than 15 cm in length were tested by pipetting "sea-star water" over the foot and epipodium; no reaction was displayed to this water or to sea water which had not been in contact with sea stars. A total of 66 animals were tested.

Responses to Contact

Contact with the tube feet of *Pisaster ochraceus* resulted in the same types of responses with *Haliotis rufescens* as observed with *H. assimilis*. However, there were several differences. While the response pattern began with the extension of the cephalic tentacles upon contact, touching the epipodial tentacles with the tube feet elicited a response resembling the mantle response of *Diodora aspera*, in which the mantle moves up over the shell (MARGOLIN, 1964a); in the case of the abalone the epipodium was extended up over the shell margin toward the medial line. Stimulation of the left lateral epipodial tentacles resulted in an extension of the left epipodial margin and of the right margin when the right lateral tentacles were touched. Stimulation of the posterior epipodial tentacles produced a strong reaction extending over the entire posterior area. Plate 50, Figure 4 shows *H. rufescens* exhibiting this last

response when stimulated by *Pycnopodia helianthoides*. The epipodium was withdrawn soon after contact with the epipodial tentacles ceased. This last response differs from the response observed when the posterior respiratory tentacle was touched by tube feet; in this case the epipodium was strongly extended up over the shell toward the respiratory pores. The response was rapid and the epipodium remained covering the shell for a period of time without further stimulation. The same result could be obtained by introducing extended tube feet into the posterior pore. Stimulation of the anterior respiratory tentacle or pore did not produce the same results; a slight movement of the anterior epipodium was seen but it did not match the former reaction in strength or time. Stimulation of the cephalic tentacles produced a recoil response, and no movement of the epipodium. Plate 50, Figure 5 shows the response when the posterior respiratory tentacle was touched by the tube feet of either *Pisaster ochraceus* or *Pycnopodia helianthoides*. This response is much more pronounced than the stimulation of the left lateral epipodial tentacles.

The flight pattern also differed from that of *Haliotis assimilis* in that *H. rufescens*, when touched by the tube feet of *Pisaster ochraceus*, exhibited shell twisting of a violent nature before flight. Flight responses when begun resembled those of *H. assimilis* with *Pycnopodia helianthoides* except that the responses of mucus emission and climbing did not result unless additional stimulation with the tube feet was made during flight. Touching either the foot or the epipodium of *H. rufescens* with tube feet gave no response; the tube feet withdrew from the exposed surfaces. Figure 2, Diagram c illustrates the responses of *H. rufescens* when contacted with the tube feet. This diagram shows clearly a correlation between the increasing size of the abalone and a tolerance to contact with the tube feet of the star. Animals in the 3 mm to 5 cm range showed reactions from 5 to 10 in strength. Specimens in the 5 cm to 10 cm range had mixed responses, about 50% responding strongly (5-10 in strength) while the others responded weakly (5-0). Abalones of 10 cm to 15 cm sizes gave weak responses, from 0 to 4 in strength, while animals above 15 cm in size exhibited very weak (3) or no response at all. Animals above 10 cm in the majority of cases clamped down at the initial stimulation (Plate 50, Figure 6) with shell twisting following continued stimu-

Explanation of Plate 51

RESPONSES TO DIFFUSED SUBSTANCES (*Haliotis assimilis* WITH *Pycnopodia helianthoides*)

Figure 7: Experimental tray
Figure 8: Start.

Figure 9: Cephalic tentacles appear.
Figure 10: Anterior locomotion.

Figure 11: Turning away.
Figure 12: Flight response.



Figure 7



Figure 10



Figure 8



Figure 11

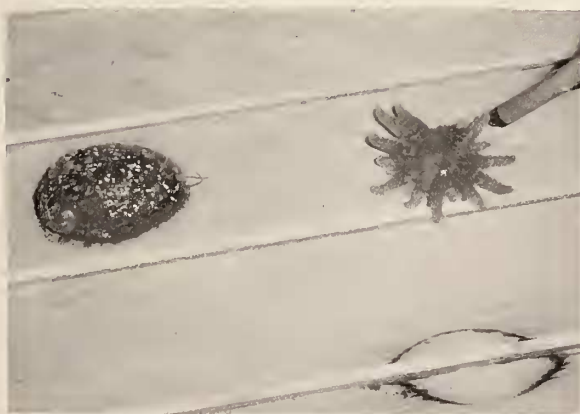


Figure 9



Figure 12

